

Limb Morphology, Bipedal Gait, and the Energetics of Hominid Locomotion

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ABSTRACT How viable is the argument that increased locomotor efficiency was an important agent in the origin of hominid bipedalism? This study reviews data from the literature on the cost of human bipedal walking and running and compares it to data on quadrupedal mammals including several non-human primate species. Literature data comparing the cost of bipedal and quadrupedal locomotion in trained capuchin monkeys and chimpanzees are also considered. It is concluded that increased energetic efficiency would not have accrued to early bipeds. Presumably, however, selection for improved efficiency in the bipedal stance would have occurred once the transition was made. Would such a process have included selection for increased limb length? Data on the cost of locomotion vs. limb length reveal no significant relationship between these variables in 21 species of mammals or in human walking or running. © 1996 Wiley-Liss, Inc.

Hominids are unique among mammals in possessing an erect, striding bipedal gait. The evolution of bipedal posture and locomotion has long been thought to be a key event in hominid evolution, so it is not surprising that considerable attention has focused on the selective influences that produced this change in posture. Possible advantages of bipedalism and erect posture are manifold, and include 1) increased visual range (Day, 1977; Ravey, 1978); 2) decreased heat load (Wheeler, 1984); 3) ease of transporting food and/or offspring (Du Brul, 1962; Jolly, 1970; Wrangham, 1980; Sinclair et al., 1987); and 4) bipedal social displays (Jablonski and Chaplin, 1993; see Rose, 1991 for a summary of various suggested agents of selection). However, one of the most popular arguments for the origin of bipedalism has involved putative effects on locomotor efficiency, measured as the rate of energy consumed to travel for a given time or distance per unit mass.

Several workers (Rodman and McHenry,

1980; Pilbeam, 1986; Foley, 1992; McHenry, 1991a) have supposed that selection for increased locomotor efficiency may have been a primary force in the origin of bipedalism in hominids. Alexander (1991), Rose (1991), and Jablonski and Chaplin (1993) have questioned the relative efficiency of human bipedality, suggesting that some factor(s) other than locomotor efficiency must have been important in the origin of erect posture. The relative inefficiency of human running has also been pointed out by Carrier (1984).

A related series of questions involving the significance of hindlimb length in early hominids has also remained unresolved. Humans are exceptional for both their long hindlimbs and their great endurance, and some workers have at least tacitly assumed a functional relationship between these two traits. Is there a relationship between loco-

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motor efficiency and relative hindlimb length? If so, would the shorter hindlimbs characteristic of early hominids (Jungers, 1982, 1991; Jungers and Stern, 1983) have resulted in lower efficiency, and favored the evolution of longer limbs in later hominids?

This paper addresses the relative locomotor efficiency of bipeds vs. quadrupeds by analyzing data from previous studies on the cost of locomotion in humans, non-human primates, and a variety of other mammals. These data are then used to assess the validity of the hypothesis that energetic efficiency was an important selective force in the origin of hominid locomotion. In addition, an analysis of the relationship between relative limb length and energetic efficiency is presented as a basis for evaluating the hypothesis that energetic efficiency favored an increase in relative limb length in hominids.

HOW EFFICIENT IS HUMAN LOCOMOTION?

Several studies have examined the energetics of modern human locomotion (Margaria et al., 1963; Cotes and Meade, 1960; Knuttgen, 1961; Dill, 1965; Menier and Pugh, 1968; Van der Walt and Wyndham, 1973; Zarrugh et al., 1974; Cavanagh and Williams, 1982; Zarrugh and Radcliffe, 1978). In most mammalian species the energetic cost of locomotion has been found to increase linearly with speed (Taylor et al., 1970, and see summary in Taylor et al., 1982), even across gait transitions (although see Hoyt and Taylor, 1981, and Parker et al., 1984). Humans differ in that cost increases curvilinearly with speed in walking (Margaria et al., 1963; Cotes and Meade, 1960) but linearly with speed in running (Margaria et al., 1963; Knuttgen, 1961; Dill, 1965).

In discussions of energetic efficiency it is probably most relevant to think in terms of the cost to travel a given distance (the cost of transport) rather than for a given amount of time (the cost of locomotion). This convention has the additional advantage of taking into account species differences in the Y intercepts of linear functions. Figure 1 shows estimates of the cost of transport for a person to walk at optimal speed (1.25 ms^{-1} , Ralston, 1976, Margaria et al., 1963, and used by Rod-

man and McHenry, 1980), or to run at $3.83 \text{ ms}^{-1} = 8.6 \text{ mph}$, a speed at which humans can readily cover very substantial distances, based on data from the literature (Cotes and Meade, 1960; Margaria et al., 1963; Knuttgen, 1961). These values are compared to the predicted costs for typical mammals based on the equations in Taylor et al. (1982). As is immediately apparent from the figure, the cost of transport for *running* humans is consistently above that of a typical mammal, though not as much above as suggested by Carrier (1984). Human *walking*, on the other hand, is more efficient than that of a quadruped for the same mass and speed. Thus human walking is more efficient than quadrupedal locomotion while human running is less efficient. Alexander (1991) came to a similar conclusion, although he argued that humans do not seem remarkably economical even at walking speeds. Fedak et al. (1974) estimate that human running is about 25% less efficient than human walking based on Margaria et al. (1963). Tucker (1975) also noted that human walking is more efficient than human running.

One should bear in mind, however, that an understanding of the efficiency of human locomotion may involve issues other than that of our unique form (among mammals) of bipedal locomotion. Taylor et al. (1982) summarize data on locomotor cost in a variety of mammals and calculate the percentage differences for each species between the observed and predicted rates of oxygen consumption. Quite a few quadrupeds show greater deviations from the predicted value than do humans. Thus, we cannot assume that the high cost of human running or the low cost of human walking is necessarily a consequence of bipedality.

WAS LOCOMOTOR EFFICIENCY IMPORTANT IN THE ORIGIN OF BIPEDALITY?

Taylor and Rowntree (1973) compared the cost of bipedal locomotion to that of quadrupedal locomotion in trained chimpanzees and capuchin monkeys. They were not able to detect an energetic difference between the two modes of locomotion and concluded that consequently the "efficiency of bipedal vs.

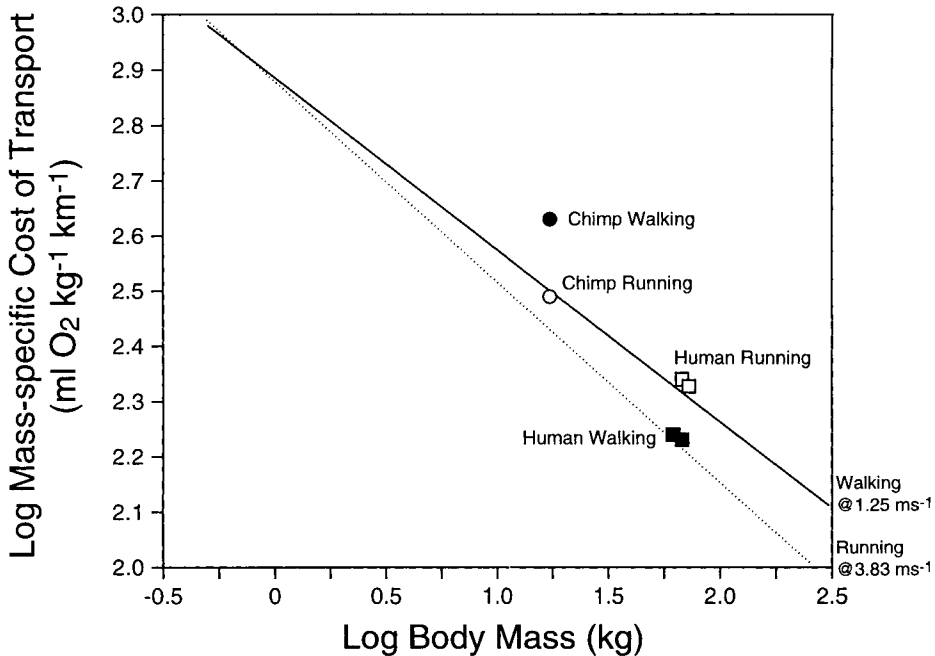


Fig. 1. The cost of walking (at 1.25 ms⁻¹) and running (at 3.83 ms⁻¹) in humans and chimpanzees in comparison to expected mammalian values (Taylor et al., 1982).

quadrupedal locomotion probably should not be used in arguments weighing the relative advantages and disadvantages that bipedal locomotion conferred on man." Rodman and McHenry (1980) took a different approach. They compared values for human vs. chimpanzee cost of transport at walking speeds and found that humans were able to travel a given distance at a lower mass-specific cost at both speeds tested. On the basis of these results, they argued that "bipedalism of living hominids is considerably more efficient than quadrupedalism of living hominoids." They go on to propose that this increased efficiency of bipedal locomotion was "an important factor in the origin of bipedalism" (see also McHenry, 1991a).

Which of these perspectives should guide our thinking about the role, if any, of energetic efficiency in the origin of bipedality? The data used by Rodman and McHenry (1980) show that the observed/predicted cost of human walking is more than 50% less than that of chimpanzee walking, suggesting a massive energetic advantage. This result, however, is driven only in part by the effi-

ciency of bipedal walking in modern humans. Taylor et al. (1982) compare the observed costs of locomotion of a wide range of mammalian species with the costs expected for an animal of a given body size. They report that the observed cost in their chimpanzees was 36% above the predicted cost (see Fig. 1); chimpanzees were among the least energetically efficient mammals that they studied. Studies on the cost of locomotion of other primates (Parsons and Taylor, 1977; Mahoney, 1980; Taylor et al., 1982) reported values much more in line with that expected of mammals of equivalent size. Chimpanzees appear to be particularly inefficient. It is not clear that this would also be true of the ancestral hominoids, the nature of whose locomotor specializations is unknown (Rose, 1991).

While, as I have indicated above, one cannot assume that the efficiency of modern human locomotion at walking speeds is due to bipedalism, it does seem reasonable to conclude that modern human walking is more efficient than that of a typical quadruped of similar mass. A perusal of Taylor et

al. (1982, pp. 10–15), however, demonstrates that many quadrupeds meet or exceed the level of efficiency seen in human walking. Becoming bipedal is not the only way to achieve energetic efficiency. Furthermore, the very substantial inefficiency of human running means that any energetic advantage only accrues at walking speeds. Modern human walking is more efficient than the walking of juvenile chimpanzees and more efficient than that of the typical mammal, but energetically equivalent to or less efficient than the locomotion of many quadrupedal mammals.

If we assume that the energetic efficiency of modern human walking is a consequence (at least in part) of our bipedal gait, can we conclude further that the energetic efficiency of bipedal striding may have been important in the origin of bipedal locomotion in our lineage? Chimpanzees, our closest living relatives, appear to be very inefficient at locomotion. If this locomotor inefficiency was also characteristic of our common ancestor, might bipedal walking have been adopted to reduce locomotor costs? Available evidence suggests not. Bipedal walking in chimpanzees is no more efficient than quadrupedal walking (Taylor and Rowntree, 1973). This result is not surprising. Chimpanzees do not possess the morphological adaptations that allow efficient bipedal striding in modern humans.

The chief mechanism promoting efficient walking in both bipeds and quadrupeds is the transfers of energy that occur between gravitational potential energy and kinetic energy of the center of mass (Cavagna et al., 1976, 1977). Gravitational potential energy stored during toe-off is converted to kinetic energy as the limb in swing phase moves forward. Such transfers are particularly efficient in bipedal striders as compared to quadrupeds (Cavagna et al., 1977; Carrier, 1984). Bipedalism in chimpanzees differs substantially from the bipedal striding of modern humans in ways that seem likely to mitigate the magnitude and symmetry of such transfers. Specifically, Jenkins (1972) reports that the principal propulsive force in chimpanzee bipedal walking is applied ahead of the hip joint in contrast to behind the hip in walking humans. Jenkins (1972)

also reports that the vertical and lateral displacements of the center of gravity are larger in bipedal chimpanzees than in humans. More recently, Tardieu et al. (1993) report that it is not the displacement of the center of mass that differs in human vs. chimpanzee bipedal walking, but the lack of a regular periodicity in chimpanzee bipedalism. The absence of periodicity severely limits the opportunities for energy transfers. Since in bipedal chimpanzees the knee does not usually pass beneath the hip joint (Jenkins, 1972), the swing phase of the unsupported leg does not have the pendular motion thought to be so important to the efficient transfer of energy (Cavagna et al., 1977; Alexander, 1991; Preuschoft and Witte, 1991).

In addition, bipedal walking in chimpanzees is accomplished with flexed knees (Jenkins, 1972), rather than the straight knees so important to modern human locomotion (Alexander, 1991). Bent knees are necessary in bipedal chimpanzees because of the ventral position of the center of mass (Robinson, 1972). A straight knee during stance phase allows walking with minor activity in the knee extensors, while bent knees generate large moments tending to flex the knee which must be balanced by muscular tension (Alexander, 1991).

Similar problems would have been faced by the first quadrupedally adapted hominoids to have begun walking bipedally. They would not initially possess the adaptations for efficient bipedality—center of mass positioned above the hindlimbs, the ability to extend the hindlimb behind the hip joint and exert propulsive force from that position, the ability to lock the knee, and the rigid foot that would allow toe off (e.g., Reynolds, 1931; Robinson, 1972; Robinson et al., 1972). It is simply not reasonable to compare the locomotor efficiency of such an animal with the mechanically very different locomotion of modern humans. Even the Afar hominids, which have obviously undergone selection for bipedal locomotion (Lovejoy, 1981; Stern and Susman, 1983), were not fully equivalent to modern humans in their locomotor anatomy (Stern and Susman, 1983; Preuschoft and Witte, 1991).

Rodman and McHenry (1980) interpret the results of Taylor and Rowntree (1973) as

demonstrating that there was no "energetic rubicon separating hominoid quadrupedal adaptation from hominid bipedalism." This is an entirely reasonable interpretation of those data. It is not reasonable, however, to argue further that our quadrupedal ancestors would have reaped an energetic advantage as they began to walk bipedally.

IS LIMB LENGTH AN INDICATOR OF LOCOMOTOR EFFICIENCY?

While locomotor efficiency is very unlikely to have been a factor tending to make our ancestors shift from a quadrupedal to a bipedal stance, it is likely that once bipedality was achieved, subsequent evolution of limb structure would have taken place based on selection of individual differences in locomotor costs. What morphological traits should we look for in fossil hominids as indicators of their degree of locomotor efficiency? Few studies have documented an actual relationship between morphology and any aspect of locomotor performance. A conspicuous exception is Garland and Janis's (1993) analysis demonstrating a significant relationship between maximal running speed and both hind limb length and metatarsal/femur ratio. What should we look for as indicators of efficiency?

Based on biomechanical theory, one would expect that increased limb length should result in a lower cost of locomotion (Strang and Steudel, 1990; Kram and Taylor, 1990; Janis and Wilhelm, 1993). This is the variable most widely discussed as an indicator of locomotor efficiency in early hominids (Jungers, 1982; Wolpoff, 1983). Increased limb length has also been thought to be an important component of cursoriality in mammals generally (Coombs, 1978; Hildebrand and Hurley, 1985; Hildebrand, 1988, although see Steudel and Beattie, 1993). Yet available data have been unable to demonstrate any relationship between limb length and the cost of locomotion other than that due to their mutual correlation with body mass.

The only actual data to suggest a direct relationship between limb length and cost are that of Fancy and White (1987), who studied variation in the energetic cost of lo-

comotion during ontogeny in caribou. They found that the mass-specific cost of locomotion for individual caribou decreased little with increasing mass once their legs neared their maximum length in the 2nd year. They did not, however, provide any statistical treatment of the variation between limb length, body mass, and cost.

Steudel and Beattie (1995) examined data on the energetic cost of locomotion, body mass, and limb length in 21 species of mammals to see whether they could demonstrate a relationship between limb length and cost. Because both cost and limb length have very high correlations with mass ($r^2 = 0.94$ and 0.95 , respectively), they will also be highly correlated with one another. To determine whether limb length and cost were correlated in some way other than that due to their mutual correlation with mass, we examined the residuals of the regression of each variable on size. We used two estimators of the cost of locomotion: 1) the mass-specific incremental cost of locomotion (the slope of the relationship between cost and speed within each species) and 2) the mass-specific cost to run at the speed of each species' trot-gallop transition. These are both measures of the cost of locomotion rather than the cost of transport. When the relationship between cost and speed can be modelled linearly, as appears to be the case in all terrestrial locomotion except human bipedal walking and saltatory locomotion, the cost of transport and the cost of locomotion become essentially equivalent measures at each body size. A change in one mandates an equivalent change in the other. In view of the non-independence of species data points resulting from their phylogenetic relatedness, we analyzed the data using the independent contrast method (Felsenstein, 1985; Harvey and Pagel, 1991; Martins and Garland, 1991; Garland et al., 1992). The phylogeny on which the analysis was based can be seen in Figure 2.

We found no significant correlation between the residual of either measure of cost and the residual of either fore or hind limb length (Fig. 3). This result was particularly surprising given the substantial variability in both limb length and cost in these data. The very similarly sized echidna (*Tachyglos-*

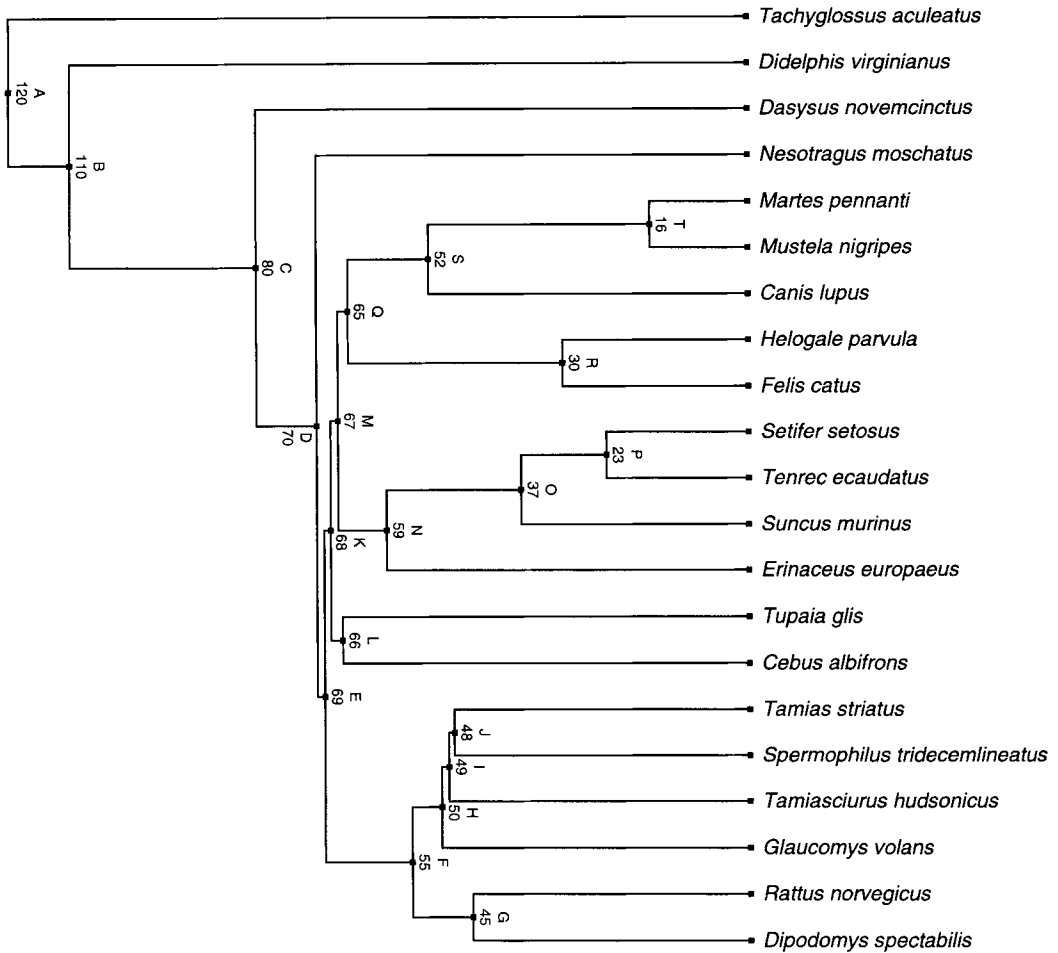


Fig. 2. Best estimates of the phylogenetic relationships among 21 species of mammals studied here. The numbers at the nodes are the estimated divergence times in millions of years B.P. The letters allow the identification of individual contrasts in Figure 3.

sus aculeatus) and suni (*Nesotragus moschatus*), for example, have limb lengths that differ by more than twofold. If limb length is an important determinant of the energetic cost of locomotion, their relationship should have been apparent in these data.

A similar result is suggested by data on both running (Cavanagh and Williams, 1982) and walking (Cotes and Meade, 1960) humans. Although neither study made a direct comparison between limb length and cost, the data necessary for such comparisons are presented. In Cavanagh and Williams (1982) limb length in 10 male runners is not significantly correlated with the mass-

specific cost to run at 3.83 m s^{-1} ($r = -0.08$, $n = 10$; see Fig. 4). Relative limb length, measured as the residual of the regression of limb length on body mass is also uncorrelated with the residual of cost on body mass ($r = -0.10$, $n = 10$). Cotes and Meade (1960) measured the cost of human walking at a variety of speeds in 10 young males and found, as had other workers (e.g., Margaria et al., 1963), that the relationship between cost and speed was curvilinear so that each individual has a speed at which his/her cost of transport is at a minimum. Regressing the minimum cost of transport against limb length reveals no significant correlation

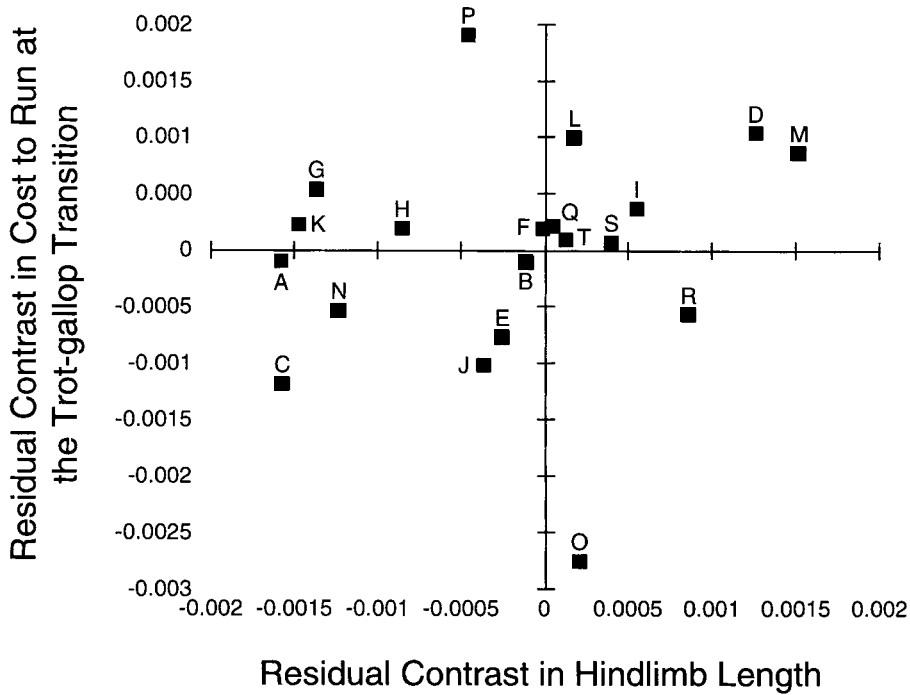


Fig. 3. The insignificant relationship between standardized contrasts in \log_{10} hindlimb length and \log_{10} cost to run at each species' trot-gallop transition speed, based on residuals from regressions through the origin of each character on \log_{10} body mass. The letter adjacent to each data point refers to the letter of the contrast indicated in Figure 2.

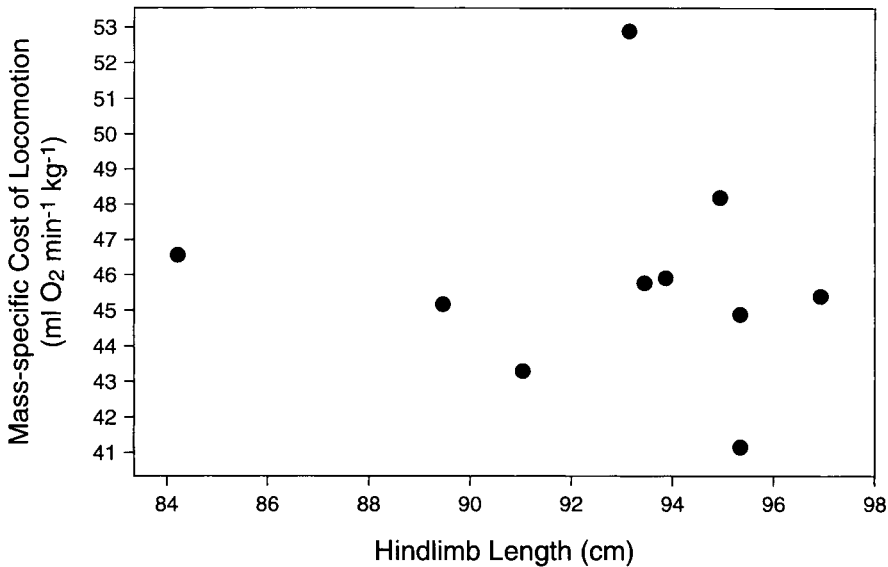


Fig. 4. The mass-specific cost of locomotion (ml O₂ min⁻¹ kg⁻¹) at 3.83 m s⁻¹ as a function of limb length (in centimeters) for 10 human subjects based on data in Cavanagh and Williams (1982). The relationship is not significant ($r = -0.08$).

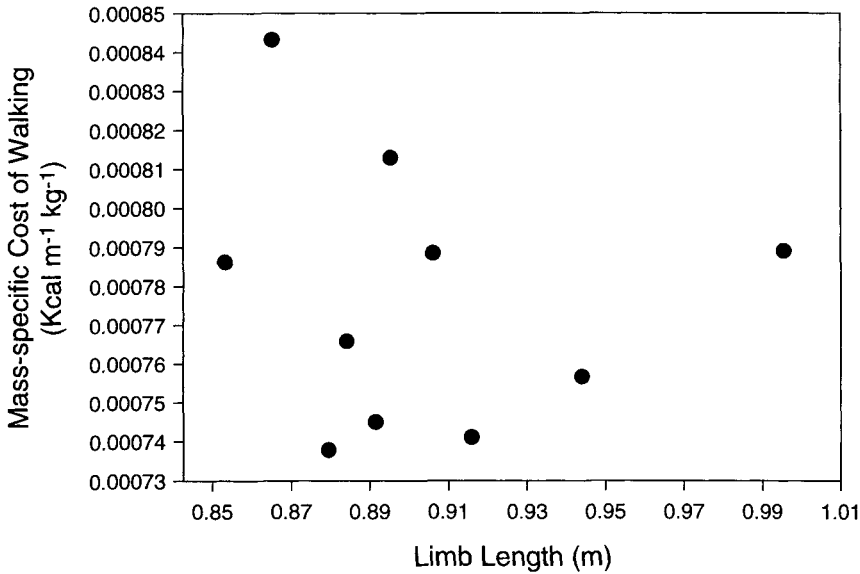


Fig. 5. The mass-specific cost of transport ($\text{kcal m}^{-1} \text{kg}^{-1}$) at each subject's lowest cost walking speed as a function of limb length (in meters) for 10 human subjects based on data in Cotes and Meade (1960). The relationship is not significant ($r = -0.16$).

($r = -0.16$; see Fig. 5). As above, residual analysis for relative limb length is also uncorrelated with the cost residual ($r = -0.08$). A Pearson's r of at least 0.63 is required for significance with $n = 10$ (Rohlf and Sokal, 1969). Inspection of Figure 5 suggests that the individual with the longest limbs might be a statistical outlier. Removal of this individual from the sample, however, resulted in a correlation that was still not significant ($r = -0.40$).

Perhaps the amount of variability in limb length among these human subjects was inadequate for revealing a modest underlying relationship. In Cavanagh and Williams (1982) the total range of variation among their human subjects was only 14% of the mean limb length. In Cotes and Meade (1960) the range of variation in limb length was 16% of the mean. There remains, however, no evidence for a relationship between locomotor cost and limb length in mammalian locomotion or in human walking or running. A possible explanation of this surprising result is suggested by the very high correlation ($r^2 = .97$) between limb length and limb moment of inertia (Steuvel, 1990). Since increases in limb moment of inertia

result in significant increases in locomotor costs (Myers and Steudel, 1985; Martin, 1985; Claremont and Hall, 1988; Steudel, 1990), it may be that increases in locomotor efficiency produced by longer limbs are balanced by decreases in efficiency due to increased moment of inertia.

EVIDENCE FOR EFFICIENCY IN "LUCY"

Even if limb length has an influence on an animal's cost of locomotion that has yet to be detected, its impact is likely to be very modest. Meanwhile, it is important to bear in mind that there is another variable that has been demonstrated to play a very important role in the determination of cost and which differs substantially between most modern humans and many early hominids—body mass. Scaling the cost of transport against body mass results in $r^2 = .95$ (slope = -0.316) for all mammals except lions and kangaroos (Taylor et al., 1982).

It becomes useful at this point to make a formal distinction between locomotor "efficiency" and "economy." Efficiency refers to the ratio of work done to energy expended (e.g. Cavanagh and Kram, 1985). Thus a

TABLE 1. Body weight and the cost of transport at 3 ms⁻¹ in extinct and extant hominids¹

Species	Body weight (kg)	Mass-specific cost of travel/meter (ml O ₂ kg ⁻¹ m ⁻¹)	Total cost of travel/meter (ml O ₂ m ⁻¹)
<i>Homo sapiens</i>	72 ³	.165	11.88
<i>Pan troglodytes</i>	45 ⁴	.192	8.62
<i>Gorilla gorilla</i>	126 ⁴	.139	17.48
<i>Australopithecus afarensis</i> ("Lucy")	30 ²	.218	6.53

¹ All values are calculated based on the summary equation in Taylor et al. (1982).

² Averages from weight estimates based on human and ape formulae (McHenry, 1991b).

³ Estimate based on data from the Cleveland Museum of Natural History.

⁴ Steudel (1985).

larger animal can be more efficient than a smaller animal if it takes more calories to travel a given distance as long as the number of calories per unit mass is less. Economy implies the thrifty use of resources. Small animals can be less efficient than larger animals but are economical because they travel further using fewer calories. Table 1 summarizes data on the efficiency (cost per kg) and economy (total cost) of locomotion for mammals of the size of modern humans, two African pongids and "Lucy." Because the focus here is on the impact of size on cost, the estimates of locomotor costs are based on the generalized mammalian equation in Taylor et al. (1982). Differences due to the locomotor adaptations of individual species are neglected. As is clear from Table 1, a mammal of Lucy's size will tend to be inefficient in comparison to larger animals. It takes a smaller mammal more energy to move a kilogram of its mass for a given time or distance. On the other hand, locomotor economy at Lucy's size compares very favorably to that of modern hominoids. The total cost for a 30 kg mammal to travel a given distance is substantially less than for a larger form.

Thus, the change in relative hindlimb length seen between Lucy and modern humans is unlikely to have had a very marked effect on locomotor energetics. The difference in body size, however, will result in major differences in cost. Lucy will have been substantially less efficient, but simultaneously more economical, than the generally larger *H. sapiens*. This body size effect will not, of course, apply simply to *Australopithecus afarensis* as a species. The level of body size dimorphism in this taxon appears to have been very substantial (Johanson and White, 1979; McHenry, 1986, 1991b). Female *A. afarensis* appear to have been substan-

tially smaller than their modern counterparts, while estimates of size in male *A. afarensis* vary from values substantially smaller than human males to values that are comparable (McHenry, 1991b). Our understanding of efficiency and economy in *A. afarensis* would, of course, be improved by greater accuracy in body mass assessments. The sex ratio of *A. afarensis* social groups and/or any gender difference in activity patterns may also be related to selection for the energetics of individual hominids and social groups.

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LITERATURE CITED

- Alexander RM (1991) Characteristics and advantages of human bipedalism. In JMV Rayner and RJ Wooten (eds.): *Biomechanics in Evolution*. Society for Experimental Biology, seminar series 36. Cambridge: Cambridge University Press, pp. 255-266.
- Carrier DR (1984) The energetic paradox of human running and hominid evolution. *Curr. Anthropol.* 25: 483-495.
- Cavagna GA, Thys H, and Zamboni A (1976) The sources of external work in level walking and running. *J. Physiol.* 262:639-657.
- Cavagna GA, Heglund NC, and Taylor CR (1977) Mechanical work in terrestrial locomotion: Two basic mechanisms for minimizing energy expenditure. *Am J. Physiol.* 233:R243-R261.
- Cavanagh PR, and Kram R (1985) The efficiency of human movement—a statement of the problem. *Med. Sci. Sports Exerc.* 17:304-308.
- Cavanagh PR, and Williams KR (1982) The effect of stride length variation on oxygen uptake during distance running. *Med. Sci. Sports Exerc.* 14:30-35.
- Claremont AD, and Hall SJ (1988) Effects of extremity

- loading upon energy expenditure and running mechanics. *Med. Sci. Sports Exerc.* 20:167–171.
- Coombs WP Jr (1978) Theoretical aspects of cursorial adaptations in dinosaurs. *Q. Rev. Biol.* 53:393–418.
- Cotes JE, and Meade F (1960) The energy expenditure and mechanical energy demand in walking. *Ergonomics* 3:97–120.
- Day MH (1977) Locomotor adaptations in man. *Biol. Hum. Affairs* 42:149–151.
- Dill WB (1965) Oxygen used in horizontal and grade walking and running on the treadmill. *J. Appl. Physiol.* 20:19–22.
- Du Brul EL (1962) The general phenomenon of bipedalism. *Am. Zool.* 2:205–208.
- Fancy SG, and White RG (1987) Energy expenditures for locomotion by barren-ground caribou. *Can. J. Zool.* 65:122–128.
- Fedak MA, Pinshow B, and Schmidt-Nielsen K (1974) Energy cost of bipedal running. *Am. J. Physiol.* 227:1038–1044.
- Felsenstein J (1985) Phylogenies and the comparative method. *Am. Nat.* 125:1–15.
- Foley RA (1992) Evolutionary ecology of fossil hominids. In E Alden Smith and B Winterhalder (eds.): *Evolutionary Ecology and Human Behavior*. New York: Aldine de Gruyter, pp. 131–165.
- Garland T Jr, and Janis CM (1993) Does metatarsal/femur ratio predict maximal running speed in cursorial mammals? *J. Zool. Lond.* 229:133–151.
- Garland T Jr, Harvey PJ, and Ives AR (1992) Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst. Biol.* 41:18–32.
- Harvey PJ, and Pagel MD (1991) *The Comparative Method in Evolutionary Biology*. Oxford: Oxford University Press.
- Hildebrand M (1988) *Analysis of Vertebrate Structure*. 3rd ed. New York: John Wiley.
- Hildebrand M, and Hurley JP (1985) Energy of the oscillating legs of a fast-moving cheetah, pronghorn, jack-rabbit and elephant. *J. Morphol.* 184:23–31.
- Hoyt DF, and Taylor CR (1981) Gait and the energetics of locomotion in horses. *Nature* 292:239–240.
- Jablonski NG, and Chaplin G (1993) Origin of habitual terrestrial bipedalism in the ancestor of the Homi-nidae. *J. Hum. Evol.* 24:259–280.
- Janis CM, and Wilhelm PB (1993) Were there mammalian pursuit predators in the Tertiary? Dances with wolf avatars. *J. Mamm. Evol.* 1:103–125.
- Jenkins F (1972) Chimpanzee bipedalism: Cineradiographic analysis and implications for the evolution of gait. *Science* 178:177–179.
- Johanson DC, and White TD (1979) A systematic assessment of early African hominids. *Science* 203:321–330.
- Jolly CJ (1970) The seed-eaters: A new model of hominid differentiation based on a baboon analogy. *Man* 5:1–26.
- Jungers WL (1982) Lucy's limbs: Skeletal allometry and locomotion in *Australopithecus afarensis*. *Nature* 297:676–678.
- Jungers WL, and Stern JT Jr (1983) Body proportions, skeletal allometry and locomotion in the Hadar hominids: A reply to Wolpoff. *J. Hum. Evol.* 12:673–684.
- Knuttgen HG (1961) Oxygen uptake and pulse rate while running with undetermined and determined stride lengths at different speeds. *Acta Physiol. Scand.* 52:366–371.
- Kram R, and Taylor CR (1990) Energetics of running: A new perspective. *Nature* 346:265–267.
- Langdon JH (1985) Fossils and the origin of bipedalism. *J. Hum. Evol.* 14:615–635.
- Lovejoy CO (1981) The origin of man. *Science* 211:341–350.
- Margaria R, Cerretelli P, Aghemo P, and Sassi G (1963) Energy cost of running. *J. Appl. Physiol.* 18:367–370.
- Mahoney SA (1980) Cost of locomotion and heat balance during rest and running from 0–55°C in a patas monkey. *J. Appl. Physiol.* 49:789–800.
- Martin PE (1985) Mechanical and physiological responses to lower extremity loading during running. *Med. Sci. Sports Exerc.* 17:427–433.
- Martins EP, and Garland T Jr (1991) Phylogenetic analyses of the correlated evolution of continuous characters: A simulation study. *Evolution* 45:534–557.
- McHenry HM (1986) Size variation in the postcranium of *Australopithecus afarensis* and extant species of Hominoidea. *J. Hum. Evol.* 15:149–156.
- McHenry HM (1988) New estimates of body weight in early hominids and their significance to encephalization and megadontia in "robust" australopithecines. In Grine FE (ed.): *Evolutionary History of the 'Robust' Australopithecines*. New York: Aldine de Gruyter, pp. 133–148.
- McHenry HM (1991a) First steps? Analyses of the postcranium of early hominids. In Y Coppens and B Senut (eds.): *Origine(s) de la Bipedie chez les Hominides (Cahiers de Paleoanthropologie)*. Paris: Editions du CNRS, pp. 133–141.
- McHenry HM (1991b) Sexual dimorphism in *Australopithecus afarensis*. *J. Hum. Evol.* 20:21–32.
- Menier DR, and Pugh LGCE (1968) The relation of oxygen intake and velocity of walking and running in competition walkers. *J. Physiol.* 197:717–721.
- Myers MJ, and Steudel K (1985) Effect of limb mass and its distribution on the energetic cost of running. *J. Exp. Biol.* 116:363–373.
- Parker KL, Robbins CT, and Hanley TA (1984) Energy expenditures for locomotion by mule deer and elk. *J. Wildl. Manage.* 48:474–488.
- Parsons PE, and Taylor CR (1977) Energetics of brachiation versus walking: A comparison of a suspended and an inverted pendulum mechanism. *Physiol. Zool.* 50:182–188.
- Pilbeam D (1986) Distinguished lecture: Hominoid evolution and hominoid origins. *Am. Anthropol.* 88:295–312.
- Preuschoft H, and Witte H (1991) Biomechanical reasons for the evolution of hominid body shape. In Y Coppens and B Senut (eds.): *Origine(s) de la Bipedie chez les Hominides (Cahiers de Paleoanthropologie)*. Paris: Editions du CNRS, pp. 59–76.
- Ralston HJ (1976) Energetics of human walking. In RM Herman, S Grillner, P Stein, and D Stuart (eds.): *Neural Control of Locomotion*. New York: Plenum, pp. 77–98.
- Ravey M (1978) Bipedalism: An early warning system for Miocene hominoids. *Science* 199:372.
- Reynolds E (1931) The evolution of the human pelvis in

- relation to the mechanics of erect posture. *Papers of the Peabody Museum of American Archaeology and Ethnology, Harvard University* 11:251–334.
- Robinson JT (1972) *Early Hominid Posture and Locomotion*. Chicago: University of Chicago Press.
- Robinson JT, Freedman L, and Sigmon BA (1972) Some aspects of pongid and hominid bipedality. *J. Hum. Evol.* 1:361–369.
- Rodman PS, and McHenry HM (1980) Bioenergetics and the origin of hominid bipedalism. *Am. J. Phys. Anthropol.* 52:103–106.
- Rohlf FJ, and Sokal RR (1969) *Statistical Tables*. New York: W.H. Freeman.
- Rose MD (1991) The process of bipedalization in hominids. In Y Coppens and B Senut (eds.): *Origine(s) de la Bipedie chez les Hominides (Cahiers de Paleoanthropologie)*. Paris: Editions du CNRS, pp. 37–48.
- Sinclair ARE, Leakey MD, and Norton-Griffiths M (1987) Migration and hominid bipedalism. *Nature* 325:307–308.
- Stern JT Jr, and Susman RL (1983) The locomotor anatomy of *Australopithecus afarensis*. *Am. J. Phys. Anthropol.* 60:279–317.
- Steudel K (1985) Allometric perspective on fossil catarrhine morphology. In WL Jungers (ed.): *Size and Scaling in Primate Biology*. New York: Plenum, pp. 449–475.
- Steudel K (1990) The work and energetic cost of locomotion 1. The effects of limb mass distribution in quadrupeds. *J. Exp. Biol.* 154:273–285.
- Steudel K, and Beattie J (1993) Scaling of cursoriality in mammals. *J. Morphol.* 217:55–63.
- Steudel K, and Beattie J (1995) Does limb length predict the energetic cost of locomotion in mammals? *J. Zool. Lond.* 235:501–514.
- Strang KT, and Steudel K (1990) Explaining the scaling of transport costs: The role of stride frequency and stride length. *J. Zool. Lond.* 221:343–358.
- Tardieu C, Aurengo A, and Tardieu B (1993) New method of three-dimensional analysis of bipedal locomotion for the study of displacements of the body and body-parts centers of mass in man and non-human primates: Evolutionary framework. *Am. J. Phys. Anthropol.* 90:455–476.
- Taylor CR, and Rowntree VJ (1973) Running on two or on four legs: Which consumes more energy? *Science* 179:186–187.
- Taylor CR, Schmidt-Nielsen K, and Raab JL (1970) Scaling of energetic cost of running to body size in mammals. *Am. J. Physiol.* 219:1104–1107.
- Taylor CR, Heglund NC, and Maloiy GMO (1982) Energetics and mechanics of terrestrial locomotion 1. Metabolic energy consumption as a function of speed and body size in birds and mammals. *J. Exp. Biol.* 97:1–21.
- Tucker VA (1975) The energetic cost of moving about. *Am. Sci.* 63:413–419.
- Van der Walt WH, and Wyndham CH (1973) An equation for prediction of energy expenditure of walking and running. *J. Appl. Physiol.* 34:559–563.
- Wheeler PE (1984) The evolution of bipedality and loss of functional body hair in hominids. *J. Hum. Evol.* 13:91–98.
- Wolpoff MH (1983) Lucy's little legs. *J. Hum. Evol.* 12:443–453.
- Wrangham R (1980) Bipedal locomotion as a feeding adaptation in Gelada baboons and its implications for hominid evolution. *J. Hum. Evol.* 9:329–331.
- Zarrugh MY, and Radcliffe CW (1978) Predicting metabolic cost of level walking. *Eur. J. Appl. Physiol.* 38:215–223.
- Zarrugh MY, Todd FN, and Ralston HJ (1974) Optimization of energy expenditure during level walking. *Eur. J. Appl. Physiol.* 33:293–306.